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Nocturnal Vocal Activity in Captive Bottlenose Dolphins (*Tursiops truncatus*): Could Dolphins have Presleep Choruses?

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Abstract - Nocturnal vocal activity in dolphins is often thought to be associated with feeding activity. However, when no food resources are available dolphins spend their time for the most part resting/sleeping. While unihemispherically sleeping, dolphins mostly swim slowly and synchronously in close proximity with one or more other individuals. Although vocal activity is lower during resting/sleeping, dolphins are not entirely silent the entire night. However, nothing is known about the temporal patterning of vocal activity at night and its potential relation with activity in dolphins. Here we recorded the vocal activity of a group of five captive bottlenose dolphins at night while having no feeding opportunity, examined whether there was any temporal pattern and/or a relation with breathing activity, used here as an index of overall activity. The temporal pattern revealed two peaks of intense whistle activity (8 p.m. and midnight), which were followed by a strong decrease of whistle rate and a slight decrease of respiration rate. We suggest that the high vocal activity at the peak periods might indicate socializing periods and that dolphins, like many other species, show periods of increased social and vocal interactions (chorusing?) before starting to rest/sleep, maybe to ensure the synchrony of slow swimming observed in this species. These findings contribute to a better understanding of nocturnal vocal activity in cetaceans and suggest new lines of research on vocal/social activity of dolphins in relation to presleep and resting behavior.

Keywords - Nocturnal activity, Resting, Vocal activity, Breathing rate, Cetaceans

Although dolphins are intensively studied, their nocturnal behavior is still in the dark. Some wild populations (e.g., spinner dolphins, *Stenella longirostris*) are actively foraging during the night, due to the increased abundance of prey (Norris, Würsig, Wells, & Würsig, 1994; Sazima, Sazima, & Da Silva, 2003; Silva & Da Silva, 2009) that is caused by the nocturnal diel vertical migration of zooplankton (Marlowe & Miller, 1975). This increased foraging activity is associated with an increased vocal activity, possibly to recruit other individuals or maintain contact (Acevedo-Gutierrez & Stienessen, 2004; Goold, 2000; Notarbartolo di Sciara & Gordon, 1997), which was also observed in captive animals when feeding, whether at day or night (Moore & Ridgway, 1996; Powell, 1966; Therrien, Thomas, Theirren, & Stacey, 2012). However, resting/sleeping tends to predominate at night when food resources are not available,

accounting for up to 87% of the night time budget in captive bottlenose dolphins (*Tursiops truncatus*; Sekiguchi & Kohshima, 2003). Cetaceans have the particularity to have a unihemispheric sleep that enables them to remain just active enough to be able to swim slowly and breathe at surface (Lyamin, Manger, Ridgway, Mukhametov, & Siegel, 2008). Most reports therefore involve resting and sleeping without clear distinction. There is some indication of periodicity across nightly rest/sleep periods indicating a bimodal pattern of resting at night (Lyamin et al., 2008). Resting/sleeping is associated with either staying at the pool bottom, floating or (mainly) swimming slowly and synchronously in close proximity with one or more other individuals (captive animals: Gnone, Benoldi, Bonsignori, & Fogani, 2001; Sekiguchi & Kohshima, 2003) or even in tight groups called “carpet formations” (wild animals: Würsig, Wells, Norris, & Würsig, 1994). In contrast to periods of active foraging or high speed swimming, vocal activity as well as respiration rates are lower during the periods of resting/sleeping (Gnone et al., 2001; Sekiguchi & Kohshima, 2003). However, some vocal activity does occur outside feeding at night, although at limited times (Kremers, Briseño Jaramillo, Böye, Lemasson, & Hausberger, 2011). Nothing is known though of the temporal patterning of night vocal activity and its potential relation with activity in dolphins. In many social species, rest/sleep is preceded by communal vocal activity as in the sleeping clusters of Barbary macaques (Ansorge, Hammerschmidt, & Todt, 1992; Hammerschmidt, Ansorge, Fischer, & Todt, 1994) and more strikingly in the roosts of some bat (Kunz, 1982) or numerous bird species (e.g., starlings: Adret-Hausberger, 1982; Feare, 1984; Hausberger, Bigot, & Clergeau, 2008). Such communal calling is so characteristic of sleep groups and night roosts that Delvingt (1961) suggested that “it appears as a prerequisite to sleep” in such species. Different functions have been proposed for these “choruses” (i.e., peaks of relatively uncoordinated vocal activity produced by more than two individuals, e.g., Marler & Slabbekoorn, 2004), one being social communication and coordination (Adret-Hausberger, 1982; Burt & Vehrencamp, 2005; Feare, 1984; Hammerschmidt et al., 1994; Hausberger et al., 2008; Kunz, 1982; Staicer, Spector, & Horn, 1996). Interestingly choruses have been described at night in humpback whales (Au, Mobley, Burgess, & Lammers, 2000) and at sunrise in bottlenose dolphins (Powell, 1966) which, independently of a particular function, reflect the association of vocal activity and social synchrony. In dolphins, increased vocal activity tends to be associated with socializing whether feeding or not (Acevedo-Gutierrez & Stienessen, 2004; Jones & Sayigh, 2002).

In the present study we recorded the vocal activity of captive bottlenose dolphins at night while having no feeding opportunity. We examined whether there was any temporal patterning and relation with breathing activity, used here as an index of overall activity (Lyamin et al., 2008; Sekiguchi & Kohshima, 2003). Because resting/sleeping seems to be associated with synchronous slow swim, we hypothesized that there may be a pattern of increased vocal activity enabling social synchronization before quieter resting/sleeping periods. The whole night period was followed and some day recordings were used for comparison.

Method

Subjects and Housing Conditions

We studied three male (5, 10, and 25 years old) and two female (8 and 17 years old) captive-born bottlenose dolphins (*Tursiops truncatus*) in Planète Sauvage’s facility (Port-Saint-Père, France). Before they were brought together to Planète Sauvage in December 2008, the males and females respectively lived together in other delphinariums. Overall, the facility of Planète Sauvage covers over 2000 m² water surface and contains 7.5 million L salt water cleaned with ozone. The diet of the dolphins was primarily composed of fish (herring, capelin, sprat, mackerel, and blue whiting) and squid. The daily ration of 5 – 10 kg per individual (depending on its size) was given throughout the day (between 9 a.m. and 5 p.m.) during nine training and feeding sessions conducted by the dolphin trainers. Sessions included medical training (e.g., acceptance of inspection and palpation) as well as training for public presentations (e.g., jump on command).

Data Collection

We observed the dolphins at different times, between 6 p.m. and 6 a.m., during eight nights in April and May 2009 (22 hr in total). Observation sessions lasted about one hour each, were repeated 2 to 5 times per night, and were distributed over the different nights in order to cover all night hours. During observations, a Nauta SS03-10 hydrophone was connected to a Marantz PMD 670 recorder (sample rate: 44.1 kHz; resolution: 16 bit; frequency response: 15 – 20000 Hz \pm 3 dB) to record the vocalizations. This same equipment had been used during a previous study on vocal behavior and had proven sufficiently to record successfully the sounds produced in all areas of the pool. In order to assess in parallel the breathing activity of the animals, a human observer (M. B. J.), seating next to the pool, counted the number of respirations. Although visual restrictions at night did not allow observation or identification, blows were well audible and therefore useful for data collection. For subsequent analyses, data were pooled in six “time periods” lasting two hours (i.e., 6 – 8, 8 – 10, and 10 – 12 p.m., 0 – 2, 2 – 4, and 4 – 6 a.m.), leading to 2 to 6 repetitions (recordings at different nights) per time period, with an average recording duration of 221 ± 89 min per time period (for details see Table 1).

In order to put the acoustic findings from those night recordings into perspective, we also used day recordings made in the same facility with the same group and the same equipment (in late March 2009 between 10 a.m. and 5 p.m.; 4 days, 16 recording sessions with a total duration of 220 min). Unfortunately, no data on respiration activity at the same time were available for those recordings.

During day and night recordings group condition was calm, meaning that the individuals were together as a group and had been in the facility for more than three months. During the day recordings, dolphins were never observed resting. Recordings were never performed during feeding, training sessions, or public presentation and there was no interaction between dolphins and humans whether during day or night recordings.

Table 1.

Details about Acoustic Recordings for Each Time Period

Time Period	Number of Recordings on Different Nights	Total Recording Duration [min]	Number of Whistles
6 p.m. – 8 p.m.	2	151	35
8 p.m. – 10 p.m.	2	203	135
10 p.m. – 12 p.m.	6	374	89
0 a.m. – 2 a.m.	4	275	164
2 a.m. – 4 a.m.	2	140	17
4 a.m. – 6 a.m.	3	184	44
Sum	19	1327	484
Mean \pm SD	3 ± 1.6	221 ± 88.9	81 ± 59.1

Data Analysis

Whistle and respiration rates were counted for each night time period: number of whistles per 120 min (“whistle rate”) and number of respirations per 120 min (“respiration rate”). Respiration rate served as a measure of activity state, with low values indicating resting/sleeping (Sekiguchi & Kohshima, 2003; Williams & Noren, 2009). In a comparative perspective, we also calculated the day whistle rate (19.64 whistles per 120 min) and considered this as a baseline since it was comparable with the whistle rate reported in another study in a same-size group of captive bottlenose dolphins (13.62 whistles per 120 min; Therrien et al., 2012).

Statistical Analyses

All statistic calculations were done using R software (version 2.15.0, R Development Core Team, www.r-project.org). Whistle and respiration rates were compared using Chi ² tests, which were also used for pairwise comparisons (correction: False Discovery Rate (FDR); R package: RVAideMemoire). Overall whistle rate was compared between night and day using Chi ² test.

Results

A total of 484 whistles were recorded. Vocal activity varied significantly in the course of the night, revealing two peaks (Figure 1): whistle rate was significantly higher than expected by chance at 8 p.m.–10 p.m. and 0 a.m.–2 a.m. ($N = 6$; $34.89 \geq \chi^2 \geq 30.98$, $p < 0.001$), whereas it was lower than expected by chance at 6 p.m.–8 p.m. and 10 p.m.–12 p.m. and 2 a.m.–4 a.m. and 4 a.m.–6 a.m. ($N = 6$; $5.16 \leq \chi^2 \leq 20.13$, $p \leq 0.023$). The highest whistle rate (76 whistles per 120 minutes) was recorded at 8 p.m.–10 p.m. and was about five times higher than at 2 a.m.–4 a.m., when we recorded the lowest whistle rate (15 whistles per 120 min). Overall, the whistle rate was significantly higher at night (43.21 whistles per 120 minutes) as compared to the day whistle rate (19.64 whistles per 120 min; $\chi^2 = 8.83$, $p = 0.003$). Respiration rate also showed variations along the night, with an overall decrease from 6 p.m.–8 p.m. (763 respirations per 120 min, i.e., 1.27 respirations/minute/individual) to 4 a.m.–6 a.m. (574 respirations per 120 min, i.e., 0.96 respirations/minute/individual; Figure 1): the highest rates were at 6 p.m.–8 p.m. and 8 p.m.–10 p.m. ($18.30 \geq \chi^2 \geq 7.08$, $p \leq 0.016$), while the lowest were at 4 a.m.–6 a.m. ($\chi^2 = 14.19$, $p < 0.001$). A slight decrease in breathing rate was observable after each vocal peak (10 p.m.–12 p.m. and 2 a.m.–6 a.m.).

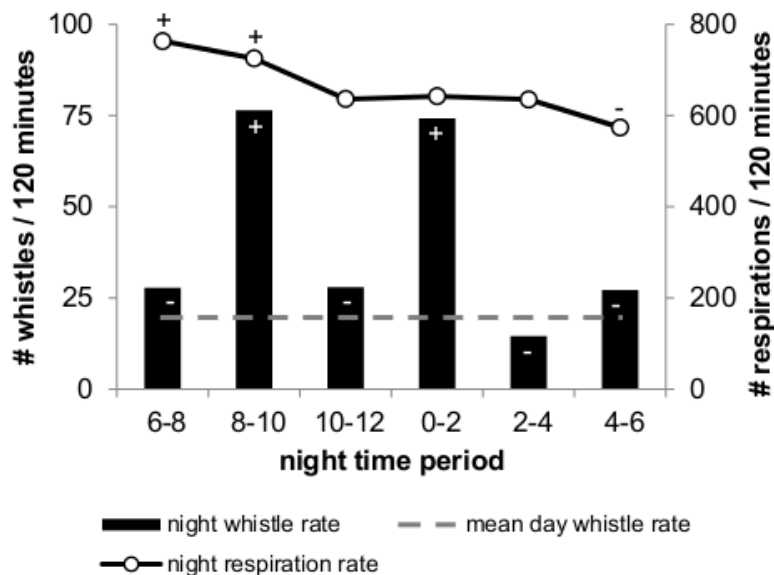


Figure 1. Changes in whistle and respiration rates in the course of the night. Whistle / respiration rates (= number of whistles and respirations, respectively, per 120 min) are illustrated with black bars/white circles. Plus- and minus-signs indicate that the observed rates are significantly higher or lower, respectively, than expected by chance (Chi ² tests; alpha = 0.05). Mean day whistle rate is illustrated as a baseline (grey dashed line)

Discussion

Nocturnal underwater acoustic recordings of a group of captive bottlenose dolphins revealed a temporal pattern with two peaks, one early at night (8 p.m. – 10 p.m.) and the other just after midnight.

Both were followed by a strong decrease of vocal activity and a slight decrease of the respiration rate. At “peak periods” the whistle rate was higher than during day recordings, which is in accordance both with the finding that some wild dolphins may whistle intensively at night (Atem & Monteiro-Filho, 2006) and that peaks in vocal activity may occur (Powell, 1966). In contrast to wild dolphins where an increased vocal activity appears to be associated with nocturnal foraging activity (Goold, 2000; Notarbartolo di Sciara & Gordon, 1997), the dolphins studied here had no feeding opportunity at night. The high rate observed here at the peak periods could indicate socializing periods as it is probable that more than one individual was involved over two hours.

Overall, breathing rates decreased overnight, especially after the two vocal activity peaks. This could correspond to an increase of resting/sleeping activity, especially since other studies also mention more resting early in the morning (Lyamin et al., 2008; Sekiguchi & Kohshima, 2003). In another study (Sekiguchi & Kohshima, 2003), rates of 0.48 to 1.05 respirations/minute/individual were observed at resting/sleeping times in captive dolphins, which is similar to the rates observed here early in the morning. Although only further and more sophisticated approaches would be needed to confirm this idea, it is admitted that lower breathing rate is associated with lower activity (Gnone et al., 2001; Sekiguchi & Kohshima, 2003) and since sleep cycle length in dolphins seems to last 1 – 2 hr (Ridgway, 2002), it could explain the occurrence of and the interval between the two vocal peaks observed.

One hypothesis issued from these data is that bottlenose dolphins, like many other species, show periods of increased social and vocal interactions before starting to rest/sleep, maybe to ensure the synchrony of slow swimming observed in captive and wild dolphins (Gnone et al., 2001; Sekiguchi & Kohshima, 2003; Würsig et al., 1994). It would then remind of the choruses observed in birds (Adret-Hausberger, 1982; Delvingt, 1961; Feare, 1984; Hausberger et al., 2008) and primates (Ansorge et al., 1992; Hammerschmidt et al., 1994) and recently described in some cetaceans (Au et al., 2000; Powell, 1966). Hence chorusing in dolphins was mentioned sporadically during behaviors that seemed to ensure behavioral synchrony and social facilitation, and was assumed to serve in cohesion (Norris et al., 1994). In any case, our findings contribute to provide further comprehension of vocal nocturnal activity in cetaceans and suggest new lines of research including a broad comparative approach of vocal/social activity of dolphins with other taxa and in relation with presleep and resting behavior.

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